Smooth pursuit performance during target blanking does not influence the triggering of predictive saccades

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Visually guided catch-up saccades during the pursuit of a moving target are highly influenced by smooth pursuit performance. For example, the decision to execute a saccade and its amplitude is driven by the difference in velocity between the eye and the target. In previous studies, we have demonstrated that the predictive saccades that occur during the blanking of the moving target compensate for the variability of the smooth pursuit response. Therefore, we wondered whether the predictive smooth pursuit response during target blanking influenced the occurrence of predictive saccades, which is the case for visually guided catch-up saccades. To answer this question, we asked subjects to track visually a target moving along a circular path. From time to time, the target was unexpectedly blanked for some randomized durations and disappeared from the screen. Surprisingly, we did not find any differences in smooth pursuit performance between the blanks that did and those that did not contain predictive saccades. In addition, during the blanks, the differences in smooth pursuit performance across the sessions or across the subjects did not correlate with the differences in the number of predictive saccades. Therefore, this study demonstrates that smooth pursuit performance does not influence the occurrence of predictive saccades. We interpret these results in light of the possible minimization of position error at target reappearance, which heavily depends on the saccadic amplitudes but not on their timing.

Keywords: eye movements, prediction, saccade-pursuit interaction, saccade trigger, smooth pursuit

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Introduction

Optimal vision of a moving object requires that the projection of this object onto the retina falls on the fovea. The function of smooth pursuit eye movements is to align the eye with a moving target. The smooth pursuit system reacts to a change in target direction or velocity with a delay of 100 ms during pursuit maintenance (Behrens, Collewijn, & Grusser, 1985; Blohm, Missal, & Lefèvre, 2005; Churchland & Lisberger, 2002; Tavassoli & Ringach, 2009). As a consequence, position error can accumulate because eye velocity does not instantly match target velocity. Two different strategies are used by the oculomotor system in order to avoid long-lasting position errors. These strategies are prediction and saccades. Prediction is used when the target trajectory is known in advance or can be extrapolated from previous information (Kowler, 1989, 1990; Kowler, Martins, & Pavel, 1984; Kowler & Steinman, 1979a, 1979b, 1981). In these cases, the oculomotor system anticipates an event before it happens. For instance, the eye velocity can increase before the onset of target motion (Barnes, Barnes, & Chakraborti, 2000). Prediction helps to minimize position error before it accumulates. In contrast, catch-up saccades are reactive and correct for an existing position error (de Brouwer, Missal, Barnes, & Lefèvre, 2002; de Brouwer, Missal, & Lefèvre, 2001). Both strategies are often used in synergy in order to optimally track a target (Orban de Xivry & Lefèvre, 2007). For example, saccades and prediction can occur together before target motion onset (Collins & Barnes, 2006) or during the blank of an ongoing moving target (Bennett & Barnes, 2003, 2006; Bennett, Orban de Xivry, Barnes, & Lefèvre, 2007; Madelain & Krauzlis, 2003; Orban de Xivry, Bennett, Lefèvre, & Barnes, 2006).

During such blank, eye velocity exponentially decays toward a plateau value (Becker & Fuchs, 1985; Mitrani & Dimitrov, 1978). The predictive smooth pursuit occurring during blanks is driven by a dynamic internal representation of target motion (Orban de Xivry, Missal, & Lefèvre, 2008). As eye velocity decreases during transient target disappearance, position error accumulates. To correct for

this before the target reappears, saccades are often generated during the blank. These saccades have been shown to bring the eye ahead of the target (Bennett & Barnes, 2003) and to compensate for the variability of the smooth pursuit response by adjusting their amplitude to the gain of the smooth pursuit response (Orban de Xivry et al., 2006). The trigger mechanism of these predictive saccades, however, has never been investigated.

The trigger mechanism of visually guided catch-up saccades, i.e., the process by which the decision of executing a saccade is taken, has been previously characterized (de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002). The decision to trigger a catch-up saccade is taken as soon as the smooth pursuit system alone cannot compensate for the position error. Whether the smooth pursuit system can or cannot compensate for the position error depends on the eye-crossing time or the time-to-contact between the eye and the target, which is the time that the eye would need to catch the target on the basis of a linear extrapolation of its current smooth motion (de Brouwer, Yuksel, et al., 2002). The decision to trigger a saccade is taken as soon as this parameter is outside the so-called smooth zone, which is larger than 40 ms or smaller than 180 ms. Therefore, during visually guided pursuit, a deficit in the smooth pursuit response causes the eye-crossing–time to leave the smooth zone and is responsible for the triggering of a catch-up saccade a few tens of milliseconds later.

During visually guided tracking of a moving target, pursuit performance influences not only the triggering of catch-up saccades as described earlier but also the amplitude of these saccades (de Brouwer et al., 2001). It has been shown that the amplitude of catch-up saccades incorporates a prediction of future target motion. Similarly, it has been demonstrated that the amplitude of predictive saccades during target blanking takes the smooth pursuit response into account (Orban de Xivry et al., 2006; Orban de Xivry et al., 2008). In contrast, using the same set of data as in Orban de Xivry et al. (2008), we demonstrate here that the triggering of the predictive saccades is not influenced by the performance of the smooth pursuit response during target blanking. Inter-session, inter-subject, and trial-to-trial analyses showed that smooth pursuit performance is not a good predictor of saccade occurrence during the blanks, such that it is not possible to predict when a saccade will be generated during the blanks on the basis of the smooth pursuit response. Therefore, we propose that this observation reflects the difference in strategy between visually guided and predictive tracking of a target.

Methods

Subjects

Six human subjects participated in the experiment after informed consent. Their ages ranged between 22 and 40 years. Four of them (S3, S4, S5, and S6) were naive regarding the goal of the experiment, and two had never participated in oculomotor experiments before (subjects S4 and S6). They all had normal or corrected-to-normal vision and did not have any known oculomotor abnormalities. All procedures were approved by the local ethics committee and were in agreement with the Declaration of Helsinki.

Paradigm

Subjects were asked to pursue a red target dot moving along a circular path (Figure 1). After having been displayed at the center of the screen for 500 ms, the target jumped toward a random position along the circular path and began to move counter-clockwise. The target first remained visible for at least half a circle (3.3 to 4 s). Then, it disappeared behind an invisible occluder three times (represented by gray bars in Figure 1) for a period ranging from 400 to 1000 ms. After each of the three blanking periods, the moving target reappeared and continued moving for a period of time ranging from 800 to 1500 ms. The target was finally switched off for about 2 s. In sum, each test trial consisted of four periods of visible target motion interlaced with three periods of blank.

Target motion varied randomly for each trial. The radius of the circular path was chosen randomly between a set of three values (9.6, 12.8, and 16 deg). In addition, the target moved along the circular path at a frequency randomly assigned from a set of three possible values (0.15, 0.2, and 0.25 Hz). The combinations of radii and frequencies led to nine different target conditions, which led to five different vectorial target velocities ranging from 9 to 25 deg/s.

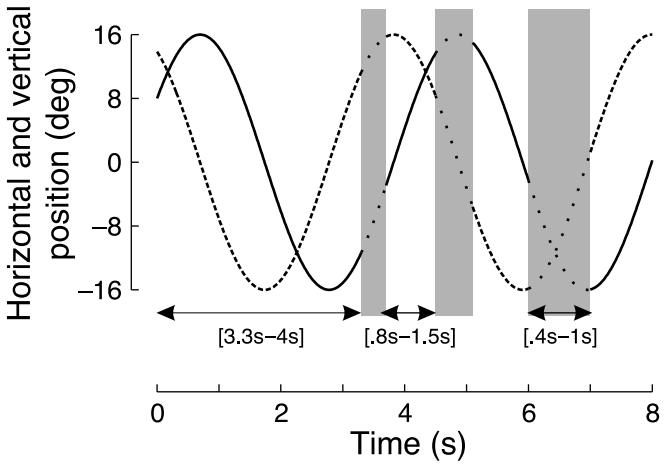

Figure 1. Horizontal (solid) and vertical (dashed) target position versus time along the circular target trajectory. During each trial, the target was blanked three times (gray areas). The blank lasted between 400 and 1000 ms. The inter-blank interval varied from 800 to 1500 ms. The period of visible target before the first blank lasted between 3300 and 4000 ms.

Experimental sessions consisted of several blocks of 13 test trials and lasted a maximum of 30 minutes. Each subject performed at least four experimental sessions, which led to a minimum of 810 blanks per subject. At the beginning of each session, a learning block was presented to the subjects. It consisted of 13 learning trials during which the visual target moved counter-clockwise on a circular path with parameters (radius and frequency) chosen in the same set as the test trials. However, the target was never switched off but remained visible for the 5-s duration of the learning trials.

Acquisition and analysis

Subjects sat in complete darkness in front of a translucent screen, which was at a distance of 1 m and covered a field of ±40 deg horizontally and vertically. The visual target was a red laser spot, which was back-projected onto the screen by two mirror galvanometers. The galvanometers were controlled by a dedicated real-time computer, which controlled their position and illumination. Eye movements were recorded using the scleral coil technique (Collewijn, van der Mark, & Jansen, 1975; Robinson, 1963).

Eye and target position were sampled at 500 Hz and stored on a hard disk for offline analysis that was performed using Matlab (Mathworks Inc., Natick, MA). Position signals were low-pass filtered using a zero-phase digital filter (autoregressive, forward, and backward filter, with a cutoff frequency of 48 Hz). Velocity and acceleration signals were derived from position by means of a central difference algorithm. Vectorial eye velocity was computed as the square root of the sum of the squared horizontal and vertical eye velocity components. Angular eye position was computed as the angular component of the polar eye position. Angular eye velocity was computed as the first derivative (central difference algorithm) of the angular eye position traces. All the trials were visually inspected to reject any trial that contained blinks. In addition, we performed an outlier analysis among the blank population in order to exclude the blanks for which the subjects stopped pursuing the target. This outlier analysis rejected all blanks for which the eye, at the target reappearance, was too far from the target or had too low of a velocity. To do so, we computed the mean and standard deviation of the vectorial position error and vectorial velocity error and rejected the trials that were more distant from the mean than three times the standard deviation for either the vectorial position or velocity errors. This led to the exclusion of 2.5% of our trials, and the total number of valid trials was 5963.

Saccades in the interval from 500 ms before the start of each blank until its end were detected using an acceleration threshold of 500 deg/s^2. The average number of saccades during the first 170 ms of the blanks was computed by dividing the number of saccades during this interval by the number of blanks for each subject separately. Similarly, the average number of predictive saccades was computed by dividing the number of saccades detected from 170 ms after the start of the blank until its end by the number of trials for each subject.

In order to analyze the saccadic latency distribution, we fitted a recinormal function to the saccadic latency distributions for each subject separately. We used a bootstrap technique with 30,000 repetitions in order to test the statistical significance of the recinormal fit. To do so, we fitted a recinormal function to 2/3 of the samples from the population and then performed a Kolmogorov–Smirnov (K-S) test in order to compare the last third of the samples with the computed recinormal function. The goodness of fit (or *p*-value) was computed as the ratio of the K-S tests that did not yield significant results and the number of K-S tests performed (30000). Before fitting a recinormal function to 2/3 of the samples from the population, we smoothed the latency distribution by means of the kernel density estimator technique (François, 2008; Parzen, 1962; Silverman, 1986), such that each data point was replaced by a Gaussian function and the sum of all these Gaussian functions yielded a continuous function (ksdensity function in Matlab). The width of the Gaussian function depended on the standard deviation of the population: $w = 1.06 \times SD \times N^{-0.2}$, where SD is the standard deviation of the population and N is the number of its elements. The fit was then estimated with the smoothed population.

Smooth eye velocity during saccades was estimated by a linear interpolation routine based on the smooth eye velocity 25 ms before and after the saccade (for further details, see de Brouwer, Missal, et al., 2002). Each eye velocity measure that was used in the following analyses (e.g., at time t) was computed by averaging the eye velocity over a 20-ms interval (e.g., from $t - 10$ ms to $t + 10$ ms). Throughout the analyses, we expressed some parameters in polar coordinates, which were noted as deg_p, and others in degree unit of visual angle, which were noted as *deg*.

Finally, we performed numerous statistical comparisons (T-tests, F-tests, and ANOVAs) between different populations using Statistica (Statsoft, Tulsa, OK). Sample means were compared using T-tests. To account for multiple comparisons, the p-values were corrected by means of the false discovery rate procedure (Curran-Everett, 2000). We performed statistical comparisons for each subject and conditions separately and thus performed 54 statistical tests (6 subjects × 3 radii × 3 frequencies).

Results

During blanks of the moving target, the vectorial smooth eye velocity decayed, and most of the time, one

or several saccades were executed (Figure 2A). In the illustrated blank, three saccades occurred (saccades "F," "S," and "T" in Figure 2A). The first one (saccade "F") brought the eye toward the center of the circle. The next two ("S" and "T") were parallel to the circular trajectory. These saccades had a completely different behavior than the visually guided saccade that was present after target reappearance (saccade "V"), which corrected for the position mismatch between the eye and the target. Indeed, the visually guided catch-up saccades that occurred after the blanks reduced the Euclidean position error (PE_{Eucl}, illustrated in Figure 2B) between the eye and the target (Figure 2C, label "V," *T*-test, $p < 0.001$ for all target velocities). The predictive saccades, however, did not reduce the PE_{Eucl}. On average, the first predictive saccade increased the PE_{Eucl} (Figure 2C, label "F," *T*-tests, $p < 0.0001$ for all target velocities), whereas the second predictive saccade did not significantly reduce PE_{Eucl} (Figure 2C, label "S," $p > 0.15$ for all target velocities). This means that the predictive saccades did not correct for the instantaneous position mismatch between the eye and the blanked target as visually guided saccades do.

Some of the features of predictive saccades are not captured by the analysis of PE_{Eucl}. For instance, the first predictive saccade brings the eye toward the center of the circle, whereas the second does not. In addition, after the first predictive saccade, the eye is ahead of the target, i.e., at a position that the target will reach, possibly after it comes out of the blank. Based on these observations, we quantified other parameters such as radial (PE_{Rad}) and angular ($PE\theta$) position errors. PE_{Rad} represents the smallest distance between the eye and the circular target path, and $PE\theta$ represents the difference in angular position between the eye and the target (Figure 2B). The analysis of PE_{Rad} confirmed that, on average, the first predictive saccade during blanks brought the eye toward the center of the circle (*T*-tests, $p < 0.0001$). In contrast, the second predictive saccade decreased PE_{Rad} for two of the five target velocities (Figure 2D, *T*-tests $p < 0.05$). In addition, the predictive saccades reduced the lag, which would lead to the reduction of $PE\theta$ after the second saccade (label "S," *T*-test, $p < 0.01$), or even generated a lead, which would lead to a negative $PE\theta$ after the first saccade (Figure 2E, label "F," *T*-tests, $p < 0.01$). The multiple comparison procedure confirmed all of the above results.

Thus, predictive saccades do not tend to reduce the position error at the time of their execution. They do, however, provide a clear advantage at the time of target reappearance. In fact, the angular position error at target reappearance was smaller for the blanks during which predictive saccades were triggered than for the blanks that were free of saccades (Figure 3, for each subject: *T*-tests, $p < 0.05$). This result is consistent with the observation that predictive saccades did not correct for the position mismatch between the eye and the target during target blanking but that they tended to minimize the sensory errors at target reappearance.

Saccade latencies

The distribution of saccade latency during the blanks was not uniform (Figure 4A). For instance, the probability of observing a saccade was similar during the pre-blank interval (visual period in Figure 4A) and during the first 100 ms of blanks. However, after this time interval, the distribution first reached a minimum 170 ms after the start of the blank before reaching a peak 120 ms later, which was 290 ms after the start of the blank. From 290 ms until the end of the blank, the probability of observing a saccade decreased gradually toward zero. It is worth mentioning that the saccade latency distribution after 400 ms must be interpreted with caution, due to the variability of the duration of the blanks. A saccade at 700 ms can only be observed in those blanks that last longer than 700 ms, but a saccade at 400 ms can be observed for all blanks. Therefore, the saccade latency distribution for the saccades with a latency period of longer than 400 ms is underestimated in Figure 4A.

In order to perform more detailed analyses, we split the saccade population into two categories. We considered the minimum of the distribution (170 ms) as the separation between visually guided and predictive saccades. The saccades that were executed before 170 ms were classified as visually guided (start period in Figure 4A). Accordingly, the saccades that occurred after 170 ms were classified as predictive saccades. The way the saccade population was segregated was consistent with the difference between predictive and visually guided saccades, as emphasized in Figure 2. The predictive saccades were also segregated into first and ensuing predictive saccades (Figure 4B). The probability of occurrence of the first predictive saccade peaked at 290 ms ($SD = 120$ ms), whereas the distribution of the ensuing saccades was more spread with a mean latency of 570 ms ($SD = 163$ ms). The spread of this distribution was reduced when saccade latency was measured relative to the previous saccade onset (245 ± 130 ms) rather than with respect to the start of the blank.

The saccade latency distribution was similar for all subjects (Figure 4C). However, the frequency of visually guided and predictive saccades varied largely between the subjects. For example, although almost three quarters of the blanks contained at least one predictive saccade, one subject (S6) exhibited very few saccades (less than 19% of the blanks). As expected, among the subjects, the average number of saccades before the blanks and during their first 170 ms was highly correlated ($r = 0.99$, $p < 0.005$). Therefore, subjects who exhibited few saccades during steady-state pursuit also executed few saccades during the first 170 ms of the blanks. Surprisingly, the average number of predictive saccades was also highly correlated with the average number of visually guided saccades

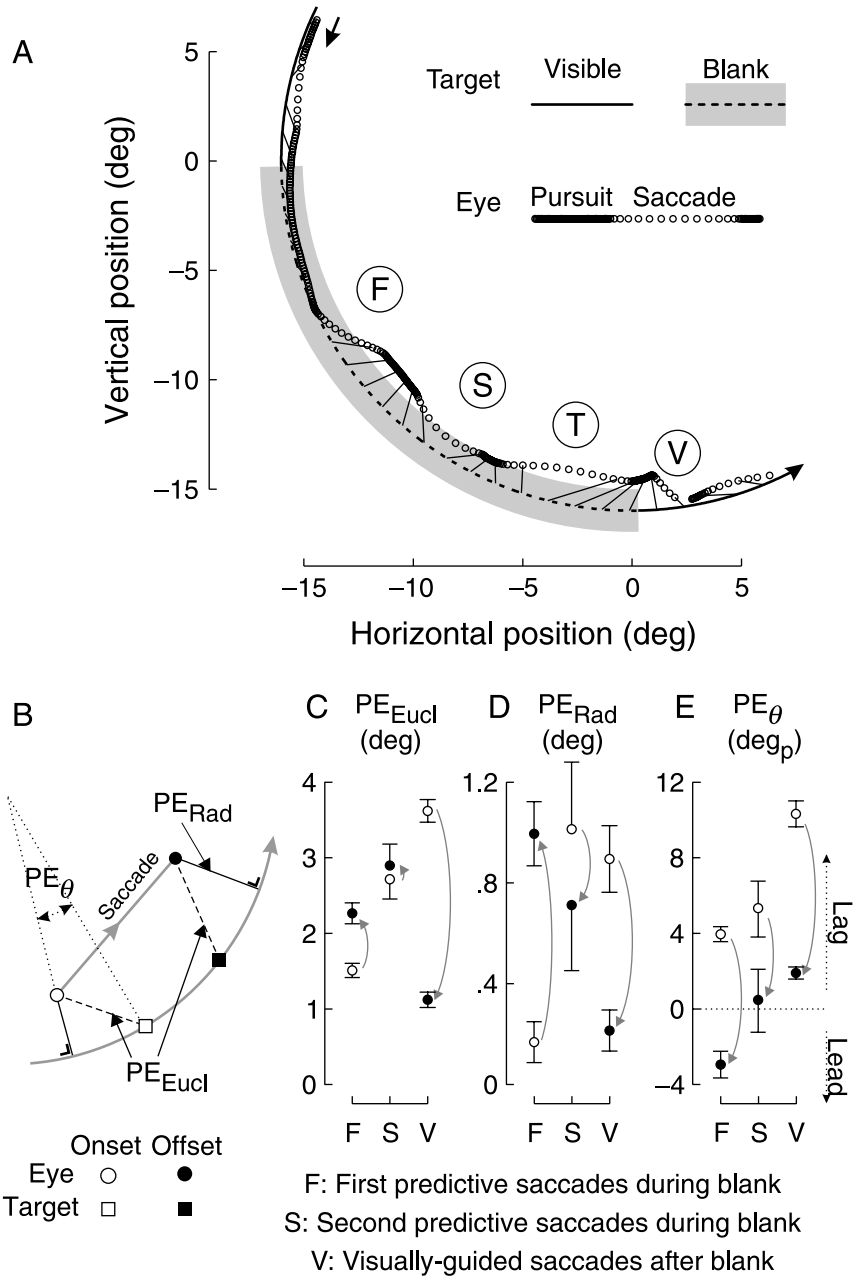

Figure 2. (A) Typical oculomotor response during blanks (horizontal vs. vertical position). The target trajectory is represented by the solid black line when the target is visible and by a dashed line over a gray area when the target is not visible. The open circles represent eye position sampled every 6 ms. Saccades are labeled F (first), S (second), T (third), and V (visually guided), and they are represented by dotted epochs on the eye trace. Eye and target positions at the same instant in time are linked by a thin black line. The origin of the reference frame coincides with the center of the circular path. Target velocity was 25 deg/s. (B–E) Evolution of different measures of position error around the time of saccades when target velocity was 25 deg/s. Schematic representation of the three error measures (B). The target path is represented by the gray arc, and the saccade by the gray arrow. Eye and target position at the moment of saccade onset (resp. offset) are indicated by an open (resp. filled) circle and an open (resp. filled) square. Mean Euclidean (PE_{Eucl}, panel C), radial (PE_{Rad}, panel D) and angular (PE_{θ}, panel E) position error (±confidence interval) for the first visually guided saccades (V) after the blanks and the first (F) and second (S) predictive saccades during the blank. Positive values of PE_{Rad} correspond to eye positions inside the circle, and positive values of PE_{θ} correspond to phase lags. The gray arrows point from measures taken at saccade onset to the same measures taken at saccade offset.

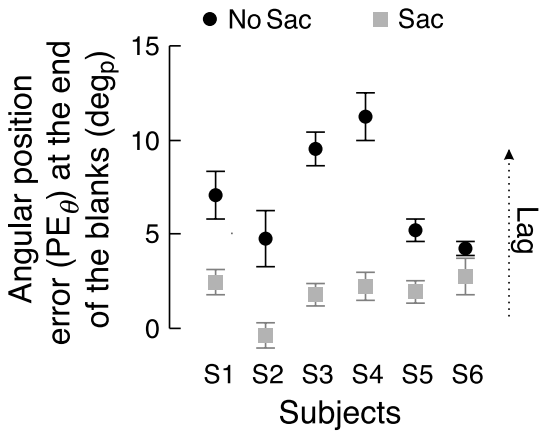

Figure 3. Influence of predictive saccades on the angular position error at target reappearance. For each subject, mean angular position error is represented in black at the end of blanks without predictive saccades and in gray at the end of blanks with predictive saccades. Spreads represent the 95% confidence intervals. The data are collapsed across all target conditions.

across our subjects (Figure 4D, $r = 0.885$, $p < 0.05$). This suggests that common mechanisms influence the occurrence of predictive and visually guided saccades.

The distributions of the first and ensuing saccades are rather skewed and possibly reminiscent of a recinormal distribution as predicted by the LATER model (Figures 4E and 4F; Carpenter & Williams, 1995). By means of the kernel density estimator and bootstrap techniques, we tested whether these distributions were recinormal (see Methods). The shape of the distribution was tested against the recinormality hypothesis for each subject separately. In order to remove the bias that occurs due to the variable duration of the blanks (see above), the blanks that lasted less than 500 ms and the saccades that occurred later than 500 ms after the start of the blank were excluded from the analysis. For the first predictive saccades, the bootstrap analysis yielded *p*-values between 0.09 and 0.16. For the ensuing saccades, the *p*-values were in the same range. The LATER model (Carpenter & Williams, 1995) states that, when an event triggers a saccade, the shape of the saccade latency distribution aligned to the time of this event is recinormal. In our study, the fact that, when the latencies are computed with respect to the time of target disappearance, their distribution has a recinormal shape suggests that the target disappearance triggers the first predictive saccades. In the following section, the putative influence of the smooth pursuit performance on saccade trigger will be systematically investigated.

Does pursuit performance influence the occurrence of the first predictive saccades?

To test the hypothesis that pursuit performance influenced the triggering of the first predictive saccades ($H_{influence}$), we separated the population of blanks into two different groups. The first was the "One Sac" group, which included blanks during which a predictive saccade was triggered within a given interval of time, and the second was the "No Sac" group, which included blanks that were free of predictive saccades during this same interval. The vectorial and angular eye velocity measured during the blanks of the "One Sac" group was compared to the same measures taken during the blanks of the "No Sac" group. For the blanks of the "One Sac" group, the vectorial and angular eye velocities were measured around 100 ms before the average latency of the predictive saccade. The measures were taken at the same time points for the "No Sac" group.

In order to have a first overview of the role of the smooth pursuit performance on the occurrence of predictive saccades, we tested whether the smooth pursuit performance at the start of the blank might influence the triggering of the first predictive saccade. Therefore, the "One Sac" group included all the blanks with a predictive saccade occurring between 200 and 400 ms (Figure 5A, lower panel), and the "No Sac" group included all the blanks that were free of predictive saccades during the first 400 ms, even if a saccade occurred later in the blank (Figure 5A, upper panel). Because the average latency of the selected first predictive saccade was 286 ms, the smooth pursuit response was measured around 100 ms earlier, which was 200 ms after the start of the blank (~286–100 ms). We postulated that, if $H_{influence}$ held, the eye velocity measured during blanks from the "One Sac" group (EV_S) should be smaller than the same measure taken during the blanks of the "No Sac" group (EV_{NS}). For one subject (S4), we determined the mean EV_S versus mean EV_{NS} for the nine different target conditions (Figure 5B). For this subject, the data points were perfectly aligned with the identity line, which was the oblique line at 45 deg_p from the horizontal. This alignment indicates that the mean EV_S and EV_{NS} did not differ, which was confirmed by the non-significance of the corresponding *T*-tests ($p > 0.05$). Therefore, the data from this subject rejected any possible influence of the smooth pursuit performance on the occurrence of the first predictive saccade. This analysis was repeated for each subject separately. Across all subjects, $H_{influence}$ was rejected in the majority of the cases (48 out of 54, *T*-tests, $p > 0.05$), which indicates that the smooth pursuit response did not influence the triggering of the first predictive saccade. In addition, when the *p*-values were corrected for multiple comparisons (see Methods), the difference between EV_S and EV_{NS} remained significant in only one single case. The same analysis was performed with the angular velocity rather than the vectorial velocity. Measures of the angular velocity 200 ms after target disappearance did not vary between the "One Sac" and "No Sac" groups in 43 of the 54 cases (*T*-tests, $p > 0.05$). In this case, the false discovery rate procedure rejected $H_{influence}$ in all of the 54 cases. The same analysis was performed on the

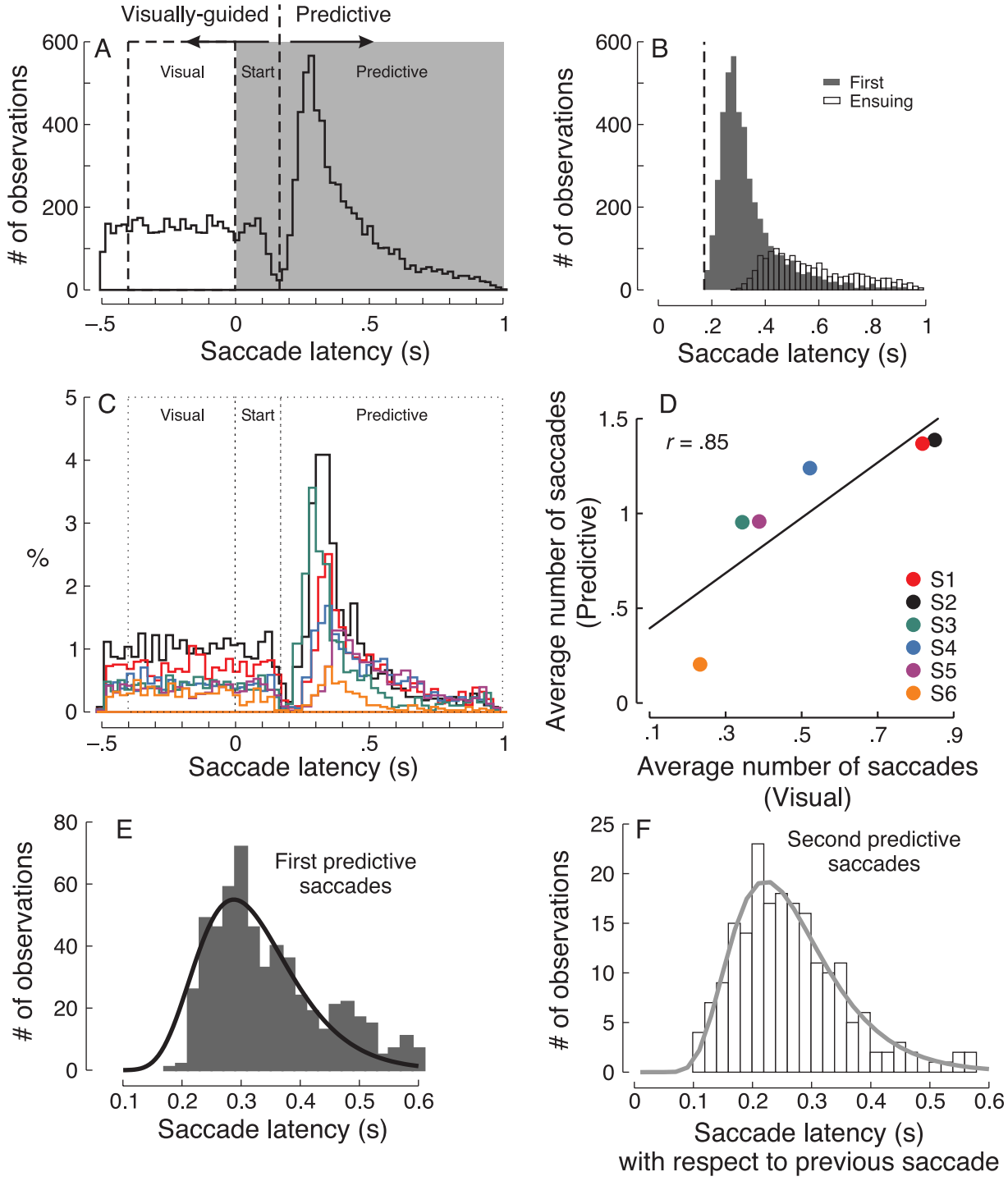

Figure 4. (A) Saccade latency distribution for all saccades occurring from 500 ms before the blank until its end. The gray area represents the blank. The dashed vertical line separates the visually guided and the predictive saccades (170 ms). Three time windows are delimited: Visual [−0.4 to 0 s], Start [0 to 0.17 s], and Predictive [0.17 to 1 s]. The data from all subjects are pooled together. (B) Saccade latency distribution of the first (dark gray) and ensuing (black outline) predictive saccades. The dashed vertical line represents the separation between the visually guided and predictive saccades as defined in panel A. (C) Same as panel A, but for each subject separately (color code given in panel D). (D) Inter-subject correlation between the average number of saccades during the Predictive period and the average number of saccades during the Visual period. (E) Latency distribution of the first predictive saccades for subject S4. The black line represents the recinormal fit. (F) Latency distribution of the second predictive saccades for subject S4. Latencies were measured relative to the onset of the previous saccade. The gray line represents the recinormal fit.

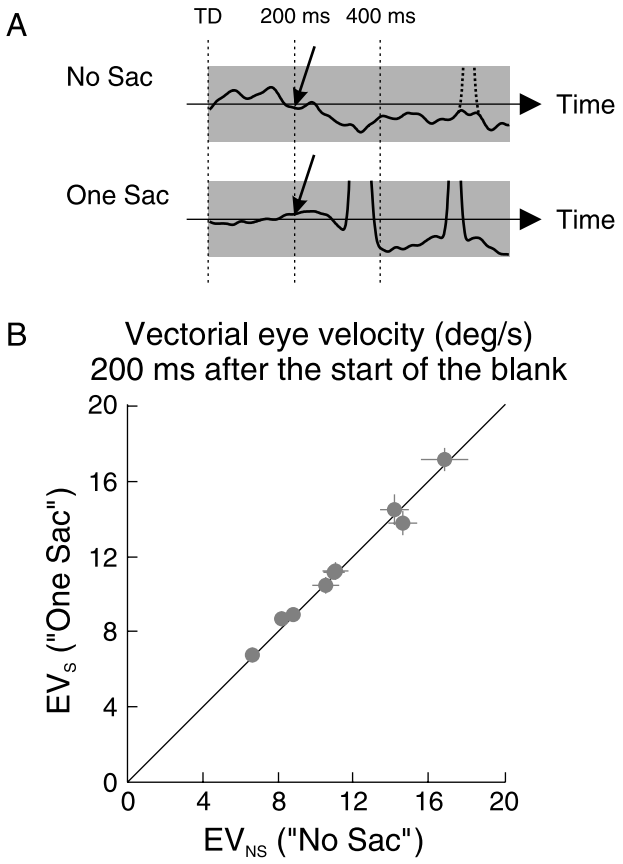

Figure 5. Comparison of the mean vectorial eye velocity 200 ms after the start of the blank (TD: target disappearance) between the blanks with their first saccade during the first 400 ms of the blank (EV_S; "One Sac") and the blanks without any predictive saccade during the same time interval (EV_{NS}; "No Sac"). (A) Schematic representation of the two groups of blanks (vectorial eye velocity vs. time). The saccades correspond to the burst in vectorial eye velocity. In the "No Sac" group (upper panel), there is no saccade between 200 and 400 ms after the start of the blank (dashed vertical lines), although there may be a saccade after 400 ms (dashed trace). In the "One Sac" group, a saccade is generated during the first 400 ms of the blank. The arrows indicate when the smooth eye velocity was measured. (B) Mean EV_S versus mean EV_{NS} for each target condition separately. Spreads indicate 95% confidence interval. The oblique line represents the identity line (no difference between EV_S and EV_{NS}). Data generated from subject S4.

vectorial velocity taken 100 ms, rather than 200 ms, after the start of the blanks, and it yielded similar results and rejected $H_{influence}$. Therefore, this analysis gave the first indication that the smooth pursuit response did not influence the triggering of the first predictive saccade when it occurred during the first 400 ms of the period of blank (rejection of $H_{influence}$). The previous analysis focused on the saccades occurring between 200 and 400 ms. In similar analyses (see Appendix A), we considered other time intervals ranging from 170 to 550 ms. Those additional analyses confirm that smooth pursuit performance does not influence the triggering of saccades throughout the whole blanking period. Therefore, these data are consistent with the hypothesis that the first predictive saccade was triggered in response to target disappearance.

In addition, if the saccade triggering were influenced by smooth pursuit performance, we would predict that their latency should depend on smooth eye velocity. Indeed, if the decision to trigger a saccade was taken later, the saccades should also occur later. As a result, saccades should be delayed during blanks with high smooth pursuit performance at their start. In other words, we tested whether a relationship exists between smooth eye velocity at the start of the occlusions and predictive saccade latency. To do so, for each subject separately, the first predictive saccades were categorized into four groups that were delimited by the quartiles of their latency distribution (Table 1). Then, the blanks that contained at least one predictive saccade were grouped accordingly, with respect to which saccade group their first predictive saccade belonged to. For each target condition, a main effect ANOVA was then performed in order to look for any difference in EV_{200} among the four blank groups. Among the 54 ANOVAs (6 subjects $\times$ 9 conditions), only five exhibited a significant difference in vectorial eye velocity among the groups of blanks ($p < 0.05$), i.e., an effect of smooth pursuit performance on the first predictive saccade latencies. In addition, two of them indicated that the saccade latency decreased with increasing EV_{200}, which is inconsistent with the hypothesis that the predictive saccade latency was influenced by smooth eye velocity. Furthermore, only four ANOVAs (out of the 54) showed a significant main effect when comparing the angular eye velocity rather than the vectorial eye velocity. Again, two of them were inconsistent with the tested hypothesis. Therefore, we did not find any evidence that the smooth pursuit performance at the start of the blank influenced the latency of the first predictive saccade, i.e., that smooth pursuit performance influenced saccade triggering.

Finally, one fourth of the blanks with predictive saccades contained more than one predictive saccade.

Subject	*N*	Q25	Q50	Q75
S1	984	0.246	0.276	0.308
S2	747	0.268	0.300	0.356
S3	852	0.230	0.260	0.304
S4	858	0.270	0.322	0.416
S5	705	0.326	0.388	0.500
S6	211	0.286	0.326	0.398

Table 1. Quartiles of the first predictive saccade latency (s) of each subject. *N* gives the number of saccades in the population for each subject. The saccades were grouped following the quartiles. Therefore, the four groups were [0.17s Q25], [Q25 Q50], [Q50 Q75], and [Q75 1s].

Therefore, we tested whether the occurrence of the ensuing predictive saccades might be determined by smooth pursuit performance. Again, we sorted out the blanks with at least one predictive saccade in two subpopulations: one with and one without a second predictive saccade. As for the first predictive saccades, we compared eye velocity measures between those two populations and did not find any significant differences that might explain the triggering of a second predictive saccade (see details in Appendix B). Therefore, we conclude that neither the first nor the second predictive saccade occurrence might be explained by the quality of the smooth pursuit response.

Inter-session and inter-subject variability

In order to investigate the influence of the smooth pursuit response on the triggering of predictive saccades, we have so far compared velocity parameters at precise time points between two populations of blanks, which were with and without predictive saccades. These analyses and others indicated that the smooth pursuit performance did not influence the triggering of predictive saccades. If this were true, we should be able to make two further observations. The first would be that an increase in the smooth pursuit gain across the different sessions should not be accompanied by a decrease in the number of blanks with predictive saccades across these sessions. The second would be that any subjects who exhibited a larger number of predictive saccades should not necessarily exhibit a lower gain of pursuit.

Given that the subjects did perform several sessions of the experiment (from 4 to 8), we expected the pursuit gain to evolve over the different sessions. In fact, the vectorial eye velocity gain at the end of the blanks did increase with the rank of the sessions (F-tests, $p < 0.05$ for each subject, all conditions pooled together). For the majority of the subjects, however, the evolution of the smooth pursuit gain, which was computed 400 ms after target disappearance, did not correspond to the evolution of the proportion of blanks without predictive saccades across sessions (Figure 6, subject S4). For five subjects, the vectorial eye velocity gain 400 ms after target disappearance increased with the rank of the session (F-test, $p < 0.05$, all conditions pooled together). For the last subject (S2), there was no significant variation of the mean pursuit gain across sessions. In contrast, the proportion of blanks without any saccade during the first 400 ms did not vary across the different sessions for three subjects (F-test, $p > 0.05$, subjects S3, S4, and S6). This proportion decreased for two other subjects (F-test, $p < 0.05$, subjects S2 and S5), and it increased in parallel with the mean pursuit gain for only one subject (F-test, $p < 0.05$, subject S1). Therefore, inter-session analyses confirmed that the frequency of predictive saccades was not related to the performance of the smooth pursuit response.

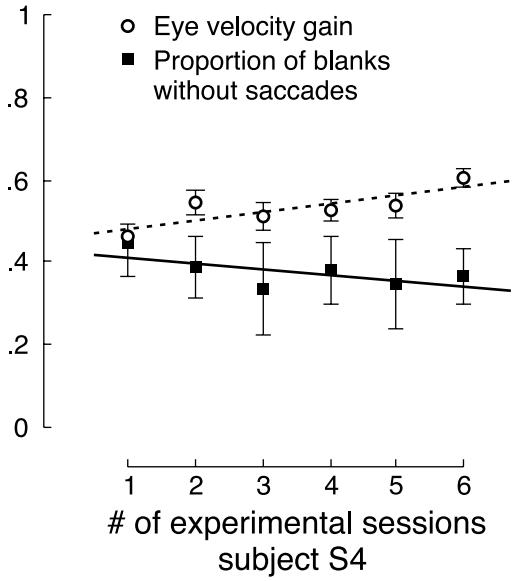

Figure 6. Evolution of the vectorial eye velocity gain (400 ms after target disappearance) and the proportion of blanks without any predictive saccade during the first 400 ms of the blank across the different sessions. Data (from subject S4) are collapsed across all conditions. Correlation between mean vectorial eye velocity gain and session number was 0.81 ($p = 0.05$), and the correlation between the proportion of blanks without predictive saccades and session number was −0.73 ($p = 0.1$).

As stated earlier, there were large differences in the proportion of blanks without saccade among our subjects (Figures 4C and 4D, from 19% to 91%). We have already observed that this proportion is correlated with the frequency of saccades during visually guided pursuit. However, we still do not know whether this proportion is also correlated with the smooth pursuit performance of the subjects during the blanks. If the smooth pursuit performance influenced the triggering of predictive saccades ($H_{influence}$), then, across subjects, the proportion of blanks without predictive saccades (Figure 7A) should be correlated with the mean pursuit gain (Figure 7B), such that the smaller the mean pursuit gain of a subject, the larger the proportion of blanks with predictive saccades. To quantify this correlation under all conditions pooled together, the pursuit gain 200 ms after the start of the blank was measured and compared with the proportion of blanks without any saccade during the first 400 ms. $H_{influence}$ did not hold among these subjects. In fact, the smooth pursuit performance across the subjects was not significantly correlated with the proportion of trials that were free of saccades (Spearman rank correlation, $p = 0.42$). We obtained similar results when we tried to correlate, across subjects, the mean pursuit gain measured at 400 ms and the proportion of blanks with at least two

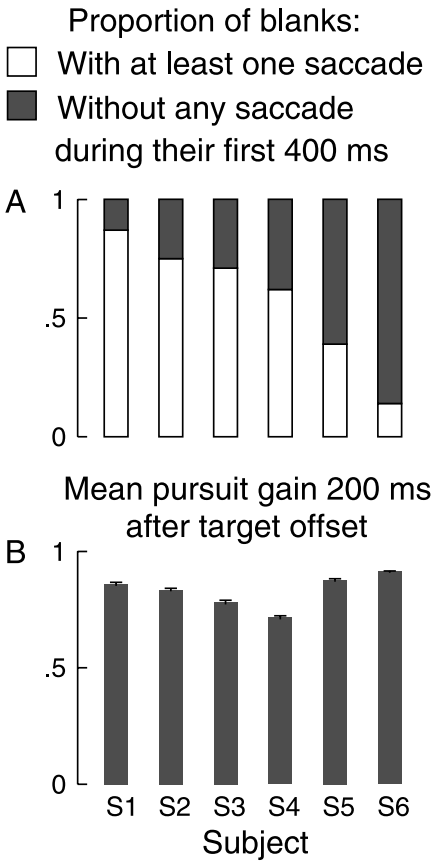

Figure 7. Inter-subject differences between the frequency of predictive saccades and the vectorial smooth eye velocity gain. All conditions are pooled together. (A) Proportion of blanks with a first predictive saccade during their first 400 ms. (B) Mean vectorial smooth eye velocity gain measured 200 ms after the start of the blanks. Spreads give the confidence interval. For panel B, the analysis was restricted to the blanks that lasted at least 700 ms.

saccades in their first 700 ms (Figure B1; details of the analysis are given in Appendix B).

Discussion

Catch-up saccades during the visually guided tracking of a moving target are highly influenced by smooth pursuit eye movements. Both their amplitude (de Brouwer, Missal, et al., 2002; de Brouwer et al., 2001) and their trigger mechanism (de Brouwer, Yuksel, et al., 2002) are based on smooth pursuit performance. We have previously shown that, when predictive saccades are present during target blanking, they compensate for the variability of the smooth pursuit response, which indicates that their amplitude is influenced by the performance of the predictive pursuit (Orban de Xivry et al., 2006; Orban de Xivry et al., 2008). Surprisingly, in the current study, we found that the occurrence of predictive saccades was independent of smooth pursuit performance. Indeed, we found that it was not possible to predict the occurrence of the first predictive saccades on the basis of smooth pursuit performance. Both the vectorial and the angular eye velocities were similar between the blanks with and without predictive saccades. In addition, we demonstrated that these measures of eye velocity did not account for whether the predictive saccade occurred early or late in the blank. Similarly, neither velocity nor position measures could predict the occurrence of the second predictive saccades. In addition, several other global variables were analyzed in order to confirm these conclusions. The evolution of the smooth pursuit gain across the different sessions did not parallel the evolution of the number of predictive saccades, as would be suggested by the hypothesis that the smooth pursuit performance influences the trigger mechanisms of predictive saccades. Finally, there was no inter-subject correlation between the smooth pursuit gain and the number of predictive saccades.

The absence of a physical occluder and the randomization of the blank durations were key aspects of our study. In this case, subjects could only rely on their dynamic internal representation of target motion during the blanks, i.e., on prediction (Orban de Xivry et al., 2008). In contrast, if there had been a physical occluder, both sensory information about target path and target position at reappearance and prediction would have driven predictive smooth pursuit and predictive saccades during the blanks. For instance, it is known that the presence of a physical occluder dramatically affects the predictive smooth pursuit response (Churchland, Chou, & Lisberger, 2003). Therefore, the presence of sensory information during the occlusion would likely affect the trigger mechanism of predictive saccades, but this remains to be tested in future experiments.

By means of an operant conditioning procedure, Madelain and Krauzlis (2003) demonstrated that it is possible to condition predictive pursuit and the occurrence of predictive saccades together. Their conditioning procedure did increase the smooth pursuit gain at the end of the blank periods and decreased the frequency of predictive saccades. Our results show that pursuit and saccades are independent to some extent during blanks. In fact, we have previously shown that the amplitude of predictive saccades is influenced by the predictive pursuit (Orban de Xivry et al., 2006; Orban de Xivry et al., 2008). In contrast, we show here that the triggering of these predictive saccades is not influenced by the predictive pursuit. These results lead to the following question: Would the conditioning of the occurrence of the predictive saccades alone influence the smooth pursuit gain? These results predict that discouraging saccades alone would not necessarily increase the smooth pursuit gain. In addition, we found that the propensity of triggering saccades during visually guided and predictive tracking was correlated across subjects (Figure 4D). This shows that there are

common control mechanisms for saccades during visually guided and predictive tracking (Darcheville, Madelain, Buquet, Charlier, & Miossec, 1999; Madelain & Krauzlis, 2003; Puckett & Steinman, 1969), i.e., subjects who triggered fewer saccades during visually guided tracking, also triggered fewer saccades during the blanks.

If the smooth pursuit behavior did not explain the presence or absence of the predictive saccades, then they should be triggered by an external event. Two different observations suggest that the first predictive saccades are triggered by the disappearance of the target. The first is the dip in the probability of observing a saccade 170 ms after the start of the blanks, which suggests that two different behaviors come into play consecutively at the start of the blanks. These behaviors are the continuation of the visually guided tracking that is pre-programmed before the blank, which is shown by the saccades during the first 170 ms of the blank, and the reaction to the disappearance of the target, which is shown by the large peak at 290 ms in the distribution of the saccade latency. After the stimulus for visually guided saccades disappeared (blank), there was initially a reduction in the frequency of visually guided saccades. At the same time, the onset of the blank initiates the process of predictive saccades generation. However, because the generation of predictive saccades occurs slightly later, there is a clear trough in the saccade latency histogram, corresponding to the transition between the two modes of response. In other contexts, a similar inhibition of the saccadic response after a change in the environment has been observed. The saccadic response is inhibited for 150 ms after the perturbation of the trajectory of one's own unseen hand that is being tracked (Ariff, Donchin, Nanayakkara, & Shadmehr, 2002) or after the perturbation of the head motion during large eye and head gaze shifts (Choi & Guitton, 2006). The second is the fact that the distribution of the first predictive saccade latencies tends to be recinormal when aligned with respect to the start of the blank. Following the LATER model (Carpenter & Williams, 1995), this would indicate that target disappearance triggered the first predictive saccade. The distribution of the second predictive saccade that was computed with respect to the onset of the first predictive saccades also tended to be recinormal, even though the size of the population did not allow for significance to be reached.

In summary, saccades that occur during predictive tracking differed from saccades that occur during visually guided tracking. During visually guided tracking, catch-up saccades are triggered on the basis of smooth pursuit response, which is the relative motion between the eye and the target (de Brouwer, Yuksel, et al., 2002). The amplitude of the catch-up saccades is correlated with the retinal slip measure that occurs 100 ms before the saccade (de Brouwer, Missal, et al., 2002; Schreiber, Missal, & Lefèvre, 2006), and these particular saccades facilitate motion processing (Schoppik & Lisberger, 2006; Wilmer & Nakayama, 2007). In contrast, during predictive tracking, saccades are not triggered by the quality of the smooth pursuit response, based on the data generated in the present study, and they do not modify the smooth pursuit response (Orban de Xivry et al., 2008). Yet, the programming of the predictive saccade amplitude does take the smooth pursuit response into account (Orban de Xivry et al., 2006; Orban de Xivry et al., 2008). All of these differences indicate that the strategies that are used during predictive and visually guided tracking are different. During visually guided tracking, humans tend to correct any predicted position error (de Brouwer, Yuksel, et al., 2002). Therefore, the smooth pursuit performance drives the trigger mechanism of visually guided catch-up saccades. In contrast, during predictive tracking, the triggering of predictive saccades is not related to smooth pursuit behavior. In fact, during blanks, the position error does not require an immediate correction since it does not cost anything. Interestingly, this change of strategy is not due to the impossibility of knowing where the target is. Internal representations of target position (Barborica & Ferrera, 2003, 2004; Filion, Washburn, & Gulledge, 1996; Orban de Xivry et al., 2008; Xiao, Barborica, & Ferrera, 2006) and eye position (Sommer & Wurtz, 2002, 2004a, 2004b; Tanaka, 2005) are available during the blank of a moving target, and yet, during predictive tracking, the saccades do not correct for a given position error. Rather, the saccades land ahead of the target in order to minimize the position error at target reappearance (Figures 2 and 3). This advance in position indicated that the subjects used the internal representation of target motion but that the actual target position yielded by this representation was not the goal of the saccade. Following optimal control theory (Todorov, 2004, 2006; Todorov & Jordan, 2002), sensory costs during visually guided tracking would be associated with poor vision related to position error and with reduced vision related to the execution of saccades. The minimization of a combination of these sensory costs would mirror the trigger mechanism of visually guided catch-up saccades (de Brouwer, Yuksel, et al., 2002). However, these costs are irrelevant during blanks, which explains why the triggering of predictive saccades is based on another mechanism. The sensory costs again become non-zero after target reappearance. Therefore, it is reasonable to hypothesize that the role of predictive saccades is to minimize the combination of sensory costs at target reappearance rather than at each time point during the blank. In this respect, the influence of the smooth pursuit performance on the timing of the predictive saccades is not relevant, whereas its influence on their amplitude is.

Appendix A

In the main text, the analysis was restricted to a subset of the first predictive saccade. To test all first saccades, the first predictive saccades were grouped into bins of latency

of 100 ms, which was followed by an evaluation of the vectorial eye velocity 50 ms before the start of the bin (100 ms before the average latency of the saccades that were included in the bin). For example, all the blanks during which the first saccade had a latency between 170 and 250 ms after target disappearance were selected (Figure A1A, middle row). For this particular group of blanks ("One Sac"), the vectorial eye velocity 100 ms after target disappearance (EV_{S100}) was measured, and this measure was compared with the measure at the same instant in time (EV_{NS100}) for the blanks without any predictive saccade ("No Sac," Figure A1A, top row). For subject S4, this comparison was illustrated by a plot of mean EV_{S100} versus mean EV_{NS100} (Figure A1, dark gray points). Each point of this plot was associated with one condition (one radius and frequency). The superposition of the points with the identity line indicates that the means did not differ, and that, for the saccades occurring between 170 and 250 ms after target disappearance, $H_{influence}$ should be rejected. On the same plot (Figure A1B, light gray points), eye velocity 400 ms after target disappearance (EV_{S400}) for a group of blanks during which the first predictive saccade occurred between 450 and 550 ms after target disappearance (Figure A1, lower row) was compared with eye velocity 400 ms after target disappearance for the same "No Sac" group (EV_{NS400}). Again, for this subject (S4), all the data points lie along the identity line, which indicates that the means of EV_{S400} and EV_{NS400} did not differ (Figure A1).

This analysis was repeated for each subject, and other time windows were investigated. To this end, four different "One Sac" groups, which included the first predictive saccade latency between 170 and 250 ms, 250 and 350 ms, 350 and 450 ms, and 450 and 550 ms and one "No Sac" group, which consisted of all the blanks without any predictive saccade, were considered. For each "One Sac" group, the eye velocity was measured 50 ms before the start of the time window (100 ms, …, 500 ms), which approximately corresponded to a period of 100 ms before the average first predictive saccade latency. Eye velocity was sampled at the same time points for the "No Sac" group. Eye velocity measurements from the "One Sac" and "No Sac" groups were then compared in order to further test $H_{influence}$. Among the 242 tested cases (5 intervals × 9 conditions × 6 subjects minus 28 cases where no saccade was detected in the time window), the vectorial eye velocity did not significantly vary between the "One Sac" and "No Sac" groups in 224 of them (93%; *T*-tests, $p > 0.05$). The significant differences did not pass the multiple comparison procedure. Accordingly, for the angular velocity, there was no difference in 220 of the 242 cases (91%). Therefore, this analysis rejected the hypothesis that smooth pursuit influenced the triggering of the first predictive saccade in more than 90% of the cases. Again, the significant differences did not pass the multiple comparison criteria. Therefore, we can conclude that the possible influence of the pursuit performance on

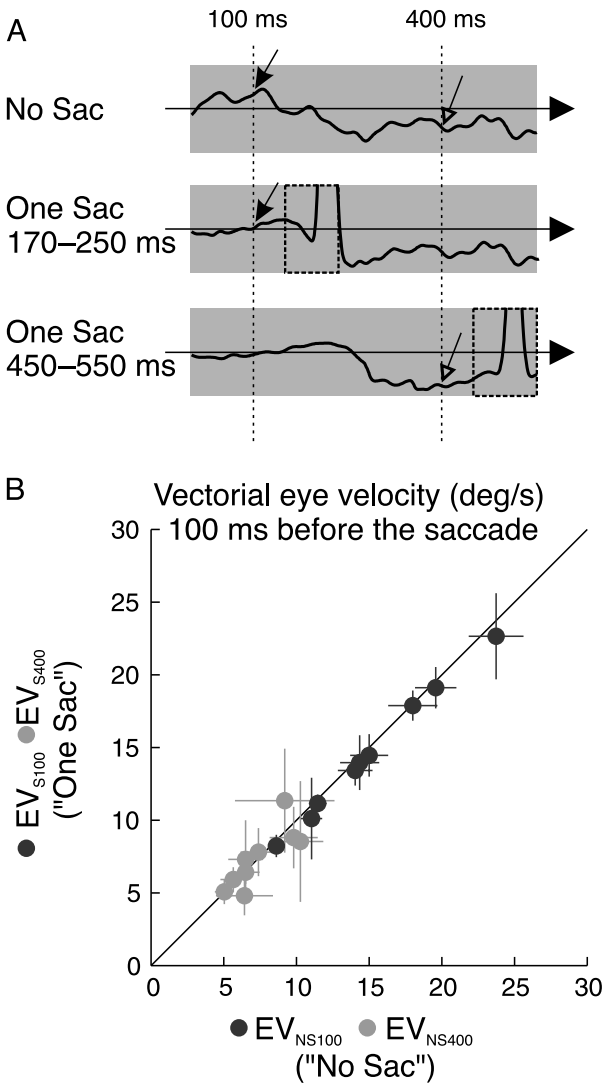

Figure A1. Comparison of the vectorial smooth eye velocity between blanks with their first saccade during a certain time interval (170 to 250 or 450 to 550 ms after target disappearance (TD)) and the blanks without any predictive saccade during the whole blank ("No Sac"). (A) Schematic representation of the different groups of blanks (vectorial eye velocity vs. time). The saccades correspond to the burst in vectorial eye velocity. "No Sac" group (upper panel) contains the blanks without any predictive saccade. Eye velocity was measured either 100 or 400 ms after TD (EV_{NS100} and EV_{NS400}). "One Sac" group (middle panel) contains blanks with the first predictive saccade occurring between 170 and 250 ms after target disappearance (dashed rectangle). Eye velocity was measured 100 ms after target disappearance (black arrows). "One Sac" group (lower panel) contains blanks with the first predictive saccade occurring between 450 and 550 ms after target disappearance (dashed rectangle). For this group, the eye velocity was measured 400 ms after target disappearance (EV_{S400}, open arrows). (B) Mean EV_{S100} versus EV_{NS100} (dark gray points) and mean EV_{S400} versus EV_{NS400} (light gray points) for each of the nine target conditions separately. Spreads indicate 95% confidence interval. Oblique line represents the identity line (no difference in velocity between the groups). Data generated from subject S4.

the predictive saccade trigger was rejected for the first predictive saccade that occurred during the first 550 ms after the start of the blank, which represents 93% of the first predictive saccade population.

Appendix B

Did pursuit performance influence the occurrence of the second predictive saccades?

Though many blanks contained at least one predictive saccade (72% of all the blanks), only 26% of them also exhibited a second predictive saccade (19% of all the blanks). This low percentage is partly due to the short amount of time remaining after the first predictive saccade, which is determined as the blank duration minus the time of saccade offset. Even when the blank lasted for more than 250 ms after the end of the first predictive saccade, which is longer than the relative latency of 66% of the second predictive saccades, the occurrence of a second predictive saccade remained low (around 38%). Therefore, we investigated why some blanks ("Two Sac") did and others ("Single Sac") did not exhibit a second saccade during a given interval of time after the first saccade (Figure B1A). This interval was set to start 75 ms after the end of the first saccade and to end 175 ms later, which corresponded to 250 ms after the end of the first predictive saccade. This limited the selection to those blanks that lasted at least 250 ms after the end of the first saccade (N = 2173). The choice of this interval also excluded any second predictive saccades that occurred later than 250 ms after the end of the first predictive saccade, which led to a rejection of 34% of the 827 second predictive saccades.

Similarly to the methods used to analyze the influence of the smooth pursuit performance on the first predictive saccades, the vectorial smooth eye velocity 50 ms after the end of the first predictive saccades between the blanks of the "Two Sac" group (EV_{TS}) were compared with the blanks of the "Single Sac" group (EV_{SS}). The eye velocity was measured 50 ms after the first predictive saccade, as this time corresponded approximately to the average inter-saccadic interval (143 ms) minus 100 ms. This analysis was performed for five of the six subjects, since the last subject (S6) rarely exhibited two predictive saccades for the same blank. Similarly to the technique used in the previous section, the mean EV_{TS} and EV_{SS} were compared for each subject and each condition separately. Again, when plotting EV_{TS} versus EV_{SS} for all the conditions of subject S4, eight of the nine data points lay on the identity line (Figure B1B). This superposition on the identity line implied that the mean of EV_{TS} and EV_{SS} did not differ for eight out of the nine conditions. The results were similar for the four other subjects. Indeed, in 38 of the 45 T-tests performed (5 subjects × 9 conditions), EV_{TS} and EV_{SS} did not differ ($p > 0.05$). When the analysis was performed with the angular eye velocity rather than the vectorial eye

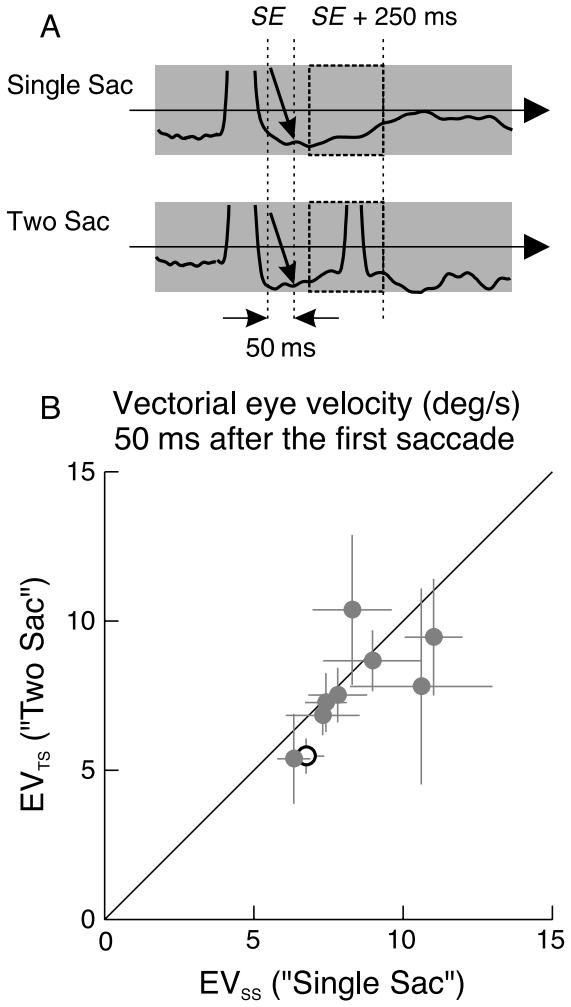

Figure B1. Comparison of the vectorial smooth eye velocity 50 ms after the end of the first predictive saccade (*SE*) between the blanks with a second saccade during the next 250 ms (EV_{TS}; "Two Sac") and the blanks with no second predictive saccade during the same interval of time (EV_{SS}; "Single Sac"). (A) Schematic representation of the two groups of blanks (vectorial eye velocity vs. time). The saccades correspond to the burst in vectorial eye velocity. "Single Sac" group (upper panel) contains blanks that did not exhibit saccades from *SE* + 75 ms until *SE* + 250 ms (dashed rectangle). "Two Sac" group (lower panel) contains the blanks during which a second predictive saccade was generated during the same time interval. The arrows indicate when the smooth eye velocity was measured (50 ms after *SE*). (B) Mean EV_{TS} versus mean EV_{SS}. Each of the nine points corresponds to one target condition. Spreads indicate 95% confidence interval. Oblique line represents the identity line (no difference between "Single Sac" and "Two Sac"). Data generated from subject S4.

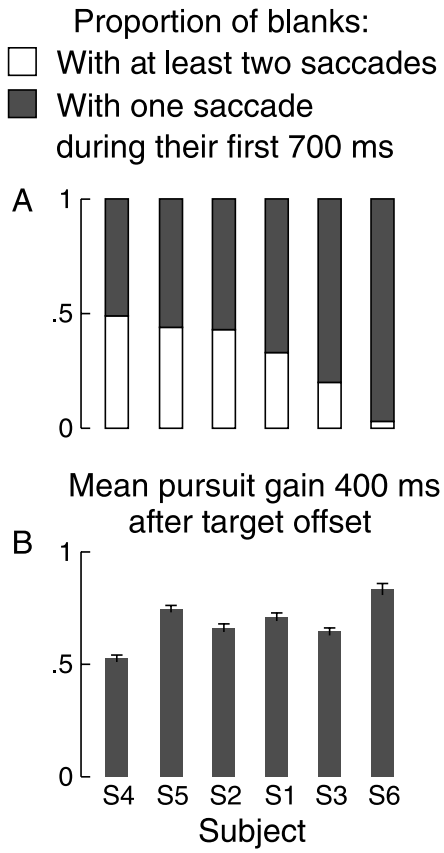

Figure B2. Inter-subject differences between the frequency of the second predictive saccades and the vectorial smooth eye velocity gain at 400 ms. All conditions are pooled together. (A) Proportion of blanks with at least two predictive saccades during their first 700 ms among the blanks with at least one predictive saccade. (B) Mean vectorial smooth eye velocity gain measured 400 ms after the start of the blanks. Spreads give the confidence interval. For panel B, the analysis was restricted to the blanks that lasted at least 700 ms.

velocity, 40 of the 45 statistical comparisons were not significant. Again, the multiple comparison procedure rejected the significance of all but one test.

Because the moment at which the eye velocity was measured depended on the latency of the first predictive saccade, we wanted to determine whether or not this parameter biased our results. The blanks were grouped with respect to the latency of their first predictive saccades (from the quartiles, see previous section). For each of the four groups of blanks, the mean EV_{TS} was tested to determine if it differed from the mean EV_{SS}, such that the level of vectorial eye velocity (respectively, angular) after the first predictive saccade influenced the triggering of a second predictive saccade. Instead, EV_{TS} and EV_{SS} were not significantly different in 139 (respectively, 140) of the 153 cases (4 groups × 9 conditions × 5 subjects minus 27 cases where one of the groups was empty). Moreover, three (respectively, seven) of the significant *T*-tests were inconsistent with the hypothesis that the level of the vectorial (respectively, angular) smooth eye velocity after the first predictive saccade was responsible for the triggering of a second predictive saccade (EV_{TS} was larger than EV_{SS}). The multiple comparison procedure rejected all significant differences for the vectorial eye velocity measures and all but one for the angular eye velocity measures.

Finally, we tested if the second predictive saccades could be elicited on the basis of the position error at the end of the first saccade. To do so, we used the same technique as above, such that the position error after the first predictive saccade was compared between the blanks of the "Single Sac" and "Two Sac" groups. Again, neither the vectorial position error nor the angular position error was found to be responsible for the generation of a second predictive saccade. In fact, the vectorial and the angular position errors were similar across the two groups of blanks ("Single Sac" vs. "Two Sac") in 43 of the 45 conditions (5 subjects × 9 conditions, *T*-tests, $p > 0.05$). The significant differences failed to pass the multiple comparison procedure.

For those second predictive saccades, we also investigated if the inter-subject variability of the quality of the smooth pursuit response might explain the variability of the occurrence of the second predictive saccades, i.e., we quantified the influence of the smooth pursuit performance on the release of the second predictive saccades. To do so, across subjects, we compared the proportion of blanks with at least two saccades in the first 700 ms of the blank (Figure B2A) with the mean pursuit gain 400 ms after the start of the blank (Figure B2B). Again, if the smooth pursuit performance influenced the release of a second predictive saccade, then the mean pursuit gain 400 ms after the start of the blank should be correlated with the proportion of blanks with a second predictive saccade during their first 700 ms. However, our data rejected this hypothesis as, across the subjects, there was no significant correlation (Spearman rank correlation, $p = 0.14$) between the proportion of blanks with several predictive saccades and the mean pursuit gain.

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